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Solanum scalarium (Solanaceae), a newly-described dioecious bush tomato from Judbarra/Gregory National Park, Northern Territory, Australia

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Abstract

A new species of functionally dioecious bush tomato of *Solanum* subgenus *Leptostemonum* is described. *Solanum scalarium* Martine & T.M.Williams, **sp. nov.**, is a member of the taxonomically challenging "Kimberley dioecious clade" in Australia and differs from other species in the group in its spreading decumbent habit and conspicuously prickly male floral rachis. The species is so far known from one site in Judbarra/Gregory National Park in the Northern Territory. Ex situ crosses and confirmation of inaperturate pollen grains produced in morphologically cosexual flowers indicate that these flowers are functionally female and the species is functionally dioecious. The scientific name reflects the ladder-like appearance of the inflorescence rachis armature of male individuals, the stone staircase that provides access to the type locality at the Escarpment Lookout Walk, and the importance of maintaining equitable and safe access to outdoor spaces. The common name Garrarnawun Bush Tomato is proposed in recognition of the lookout point at this site, a traditional meeting place of the Wardaman and Nungali-Ngaliwurru peoples whose lands overlap in this area.

Keywords

Australia, dioecy, inaperturate pollen, Judburra/Gregory National Park, new species, Northern Territory, Solanaceae, *Solanum dioicum*

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Introduction

Solanum L. is the most species-rich genus in the family Solanaceae and among the largest in the angiosperms, with ca. 1400 accepted species distributed on every continent except Antarctica (Gagnon et al. 2022). Much of the richness of the genus is concentrated in circum-Amazonian tropical South America, but other hotspots include Africa and Australia (Symon 1981; Särkinen et al. 2013; Vorontsova et al. 2013; Gagnon et al. 2022). The genus is often recognized by its pentamerous flowers with fused sepals and petals, five stamens, 2-chambered superior ovary, poricidal anthers, and, in many species, branched hairs and/or prickles (Knapp 2013). Solanums exhibit great diversity both in vegetative and reproductive traits (especially in floral and fruit traits), ecology, and reproductive biology (see Hilgenhof et al. in review).

Despite decades of research on phylogenetic relationships within *Solanum*, there is still a great deal of work to be done to fully understand the evolutionary history of this hyper diverse group. This challenge arises, in part, due to the large number of species already described within the genus coupled with a large number of species still being described. In the past decade alone, there have been more than 100 newly described *Solanum* species (see McDonnell et al. 2019). One hotspot for new descriptions over that period has been northern Australia (e.g., Brennan et al. 2006; Bean and Albrecht 2008; Barrett 2013; Martine et al. 2013, 2016a, c; Bean 2016; Lacey et al. 2017; McDonnell et al. 2019). This area is home to a clade of ca. 45 currently described species of "spiny solanums" (i.e., *Solanum* subgenus *Leptostemonum* Bitter, the Leptostemonum Clade) belonging to the *S. dioicum* + *S. echinatum* Group sensu Martine et al. (2019) (see Fig. 1 for breakdown of clade names related to this group). Key morphological characteristics of Leptostemonum Clade include the presence of stellate pubescence, stems and leaves with prickles, and attenuate anthers (Whalen 1984).

Phylogenetic work has uncovered two Australian clades (Fig. 1) of functionally dioecious *Solanum* species: the "Kakadu dioecious clade" (two species [plus one forthcoming] of the upper Northern Territory) and the "Kimberley dioecious clade" (12 species occurring from the Kimberley Plateau of Western Australia to far northwestern Queensland (Bean 2004; Martine et al. 2006; Martine et al. 2009; Martine et al. 2019; McDonnell and Martine 2020; Figs 1, 2). The "Kimberley dioecious clade" is a well-supported clade of usually clonal shrub taxa that have proven to be taxonomically challenging, ostensibly due to a complex (or at least quite recent) evolutionary history (Symon 1981; Martine et al. 2006, 2009). Species boundaries are often blurred by overlapping or intermediate morphological traits, making it sometimes difficult to distinguish taxa in the field (Symon 1981; Martine et al. 2016c); the employment of molecular phylogenetic data to address this challenge has so far resulted in poorly-resolved intraclade relationships (see Gagnon et al. 2022).

Judburra/Gregory National Park, where the new species described here is found, is floristically diverse as a result of its sandstones and limestones that have been weathered to produce deep gorges and escarpments that sustain a diversity of habitats (Australian Government Department of the Environment and Energy 2015). In recent decades

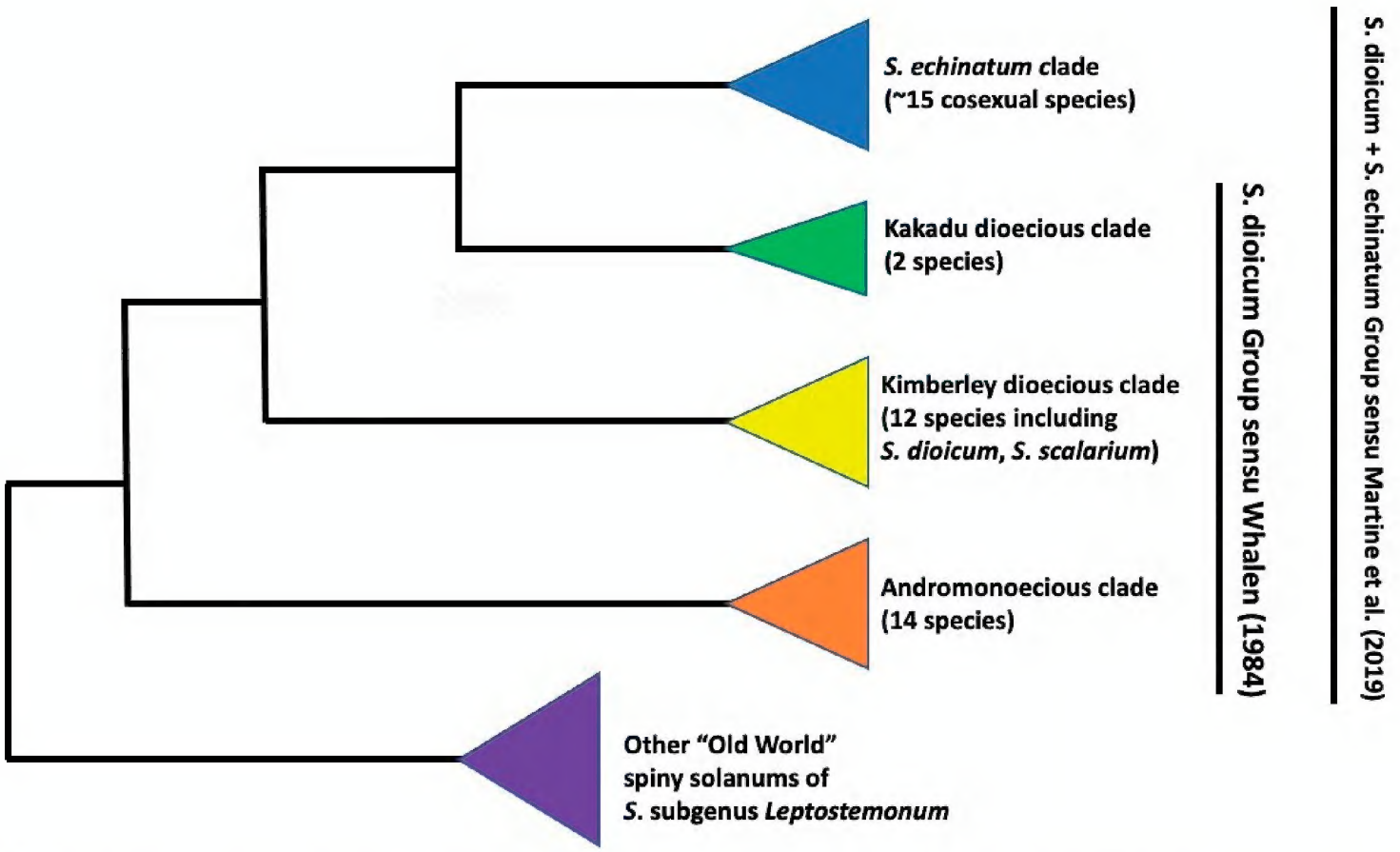

Figure 1. Representational phylogeny showing hypothesized relationships among the clades included in the "*S. dioicum* + *S. echinatum* Group" sensu Martine et al. (2019), based on that study plus forthcoming work by McDonnell and Martine (in prep). *Solanum scalarium* sp. nov. is one of twelve described species in the "Kimberley dioecious clade" sensu Martine et al. (2006), a clade of functionally dioecious species (and phrase-named morphological variants of *S. dioicum*) sometimes also referred to as the "Dioicum Complex".

the Northern Territory government has funded a number of monitoring and vegetation surveys throughout the territory. These have resulted in a series of papers describing new endemic species to the region (e.g., Craven 1998; Walsh and Albrecht 1998; Jobson 2014; Martine et al. 2016a), and others recognized as phrase-name taxa — i.e., potentially-new species recognized as distinct variants by regional field botanists (e.g., Cowie et al. 2017). On a recent collecting trip to the region as part of phylogenetic and biogeographical studies on the flora of the Australian Monsoon Tropics (AMT), a *Solanum* population was recognized as a possibly new species by CTM because of its spreading decumbent habit and its unusual staminate inflorescence axis armed with relatively stout, spreading, straight prickles (Fig. 6) and is described here as *Solanum scalarium* Martine & T.M.Williams, sp. nov. This taxon is one of the many "Kimberley dioecious clade" variants found throughout north and northwestern Australia (Symon 1981; Purdie et al. 1982; Barrett 2013).

Methods

A single fertile voucher specimen collected from the type locality included mature fruits. Once back at Bucknell University, seeds from those fruits were removed and germinated

in order to build a living collection of greenhouse plants to better assess the morphology of this putative new species. Seeds were germinated following a 24-hour soak in 1,000-ppm gibberellic acid and sown in a controlled growth chamber environment following Martine et al. (2016a). Mature plants were cultivated in an IPM-managed greenhouse following Hayes et al. (2019). Observations of the taxon by JTC, PJ, CTM, and AJM in Judbarra/Gregory National Park (NT) are combined here with measurements of characters by JH and TMW from plants grown in cultivation (Figs 4–6). The morphological description is based mostly on those cultivated individuals because of limited herbarium material of the species; data in the Australasian Virtual Herbarium and physical examination of "*S. dioicum*" holdings at the Northern Territory Herbaria (DNA, NT) suggest the species is not represented in collections beyond the type collections cited below. A map (Fig. 2) comparing the distributions of dioecious *Solanum* species in Australia was generated using records from the Australasian Virtual Herbarium.

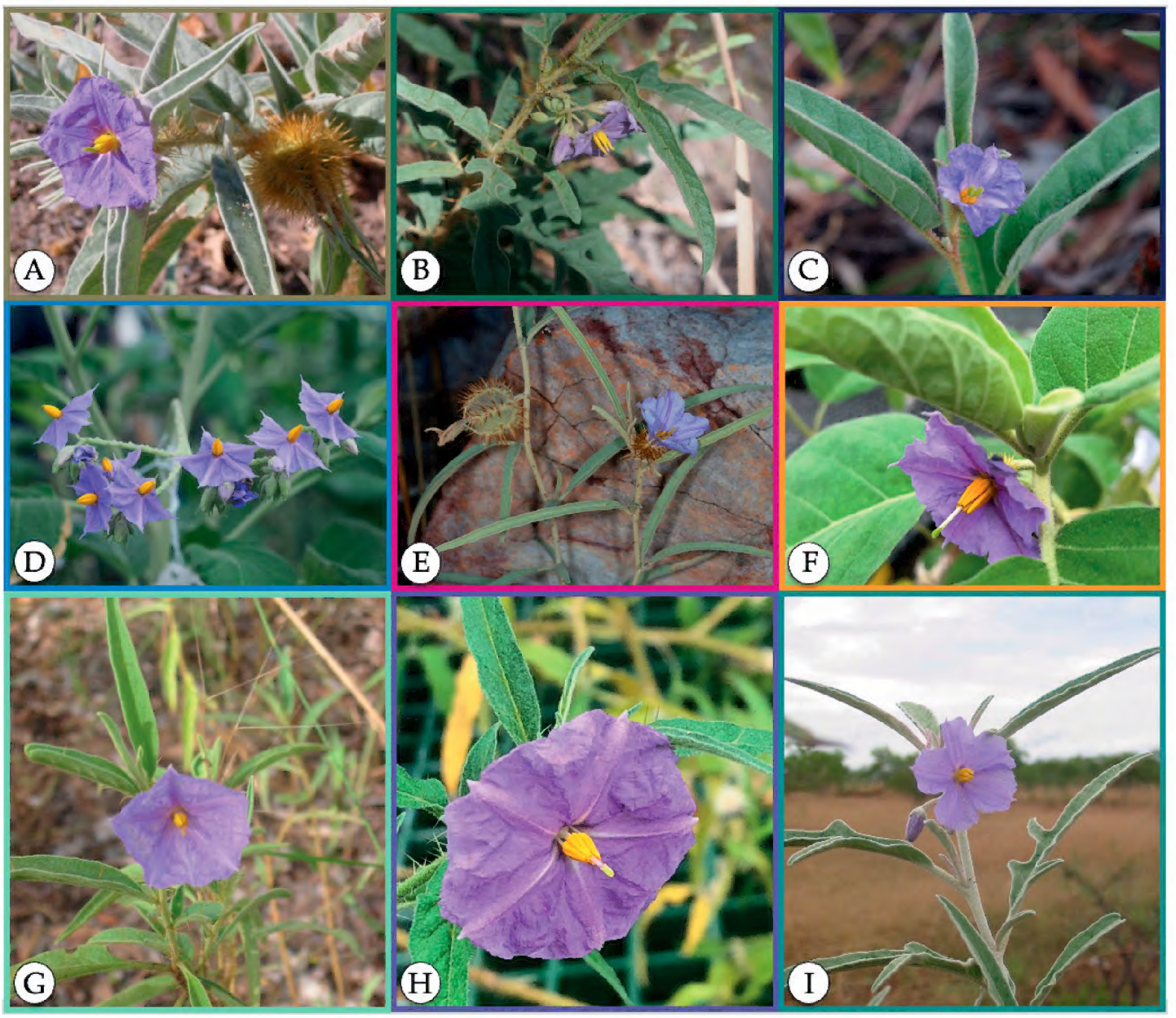

Figure 2. Functionally dioecious species of the "*S. dioicum* + *S. echinatum* Group." **A** *S. ossicruentum* Martine & J.Cantley **B** *S. carduiforme* F.Muell. **C** *S. dioicum* W.Fitzg. **D** *S. asymmetriphyllum* Specht **E** *S. cowiei* Martine **F** *S. sejunctum* K.Brennan, C.Martine & Symon **G** *S. petraeum* Symon **H** *S. leopoldense* Symon and **I** *S. tudununggae* Symon. *Solanum cataphractum* Cunn. ex Benth., *S. cunninghamii* Benth., *S. scalarium* Martine & T.M.Williams, *S. vansittartense* C.Gardner, and *S. zoeae* R.L.Barrett not pictured here. Colors are associated with the distribution map shown in Fig. 3. (Photos by C.T. Martine except for E by K. Brennan.).

Taxonomic treatment

Solanum scalarium **Martine & T.M.Williams, sp. nov.**
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Figs 4–7

Diagnosis. This species is distinguished from *Solanum dioicum* W.Fitzg. (as currently delineated) and other Australian functionally dioecious *Solanum* species of the "Kimberley dioecious clade" by the combination of a spreading decumbent habit and the staminate inflorescence axis armed with relatively stout, spreading, straight prickles.

Type. Australia. Northern Territory: Victoria River Valley, Judbarra National Park, off Victoria Highway (Highway 1), NW of Victoria River Roadhouse, Escarpment Walk, just off track above Garrarnawun Lookout on flat area between there and peak of outcrop, 15.61054°S, 131.11571°E, elev. 167 m, 2 June 2018 (fr), *C. T. Martine, J. Cantley, A. McDonnell & P. Jobson 4748* (holotype: DNA).

Description. Perennial spreading decumbent pale green shrub up to 30 cm tall. Main stem single, 4–12 cm tall, woody (not corky) branching 2–4 times with thickest lateral stems ca. 2–4 cm in diameter; younger stems yellow-green to tan-green in color and older woody stems eventually becoming dark tan or gray. Internodes 12–40 cm long in male plants, 30–46 cm long in functionally female plants. ***Stems*** with short, dense indumentum of porrect-stellate trichomes 0.5–1.3 mm, these mostly short stalked (occasionally on longer stalks up to 1 mm) with central midpoint ca. 0.2 mm. Prickles abundant and dense (8–10 per cm of internode), 1–8 mm long, straight, fine, widened at base, somewhat sharp. ***Leaves*** simple; blades 5–9 cm long, 1–3 cm wide, alternate, lanceolate; unarmed or with 1–3 straight prickles along adaxial midvein, soft yellow green above, slightly lighter beneath, both sides densely stellate-hairy, trichomes mostly short stalked, porrect-stellate with short central ray; apex acuminate; margins entire, sometimes ciliate; base oblique and tapering; petiole 0.5–14 mm long; ***Male inflorescence*** a scorpioid cyme 9–24 mm long with up to ca. 50 flowers (typically 1–4 flowers open at a time with previous blooms abscised); rachis densely stellate-pubescent, armed with straight prickles 5–7 mm, ca. 1 mm in diameter at the base, each subtending a flower; pedicel 3–7 mm long, sparsely armed with small prickles. ***Male flowers*** 5-merous; calyx with the tube 6–7 mm long, campanulate, armed with weak prickles ca. 2 mm long, the lobes 3–4 mm long, tipped with a linear acumen; corolla 16–27.4 mm in diameter, rotate to rotate-campanulate, pale violet; stamens equal; filaments 1–2 mm long; anthers ca. 4 mm long, tightly connivent, oblong-lanceolate to somewhat tapered, poricidal at the tips; ovary vestigial, non-functional. ***Female inflorescence*** of a solitary, morphologically cosexual flower (functionally female and producing inaperturate pollen); pedicel 7–8 mm long, sparsely armed with small prickles ca. 2 mm. ***Female flowers*** 5-merous; on; calyx with the tube campanulate, densely stellate-pubescent and armed, the prickles 5–6 mm long, straight, the lobes 5–11 mm long, unequal, long-triangular with a linear acumen, prickly; corolla 36–46 mm in diameter, rotate to rotate-campanulate, violet to pale violet; stamens equal, like those of the male flowers; filaments 1–2 mm long; anthers ca. 4 mm long, slightly spreading,

poricidal at the tips; ovary ca. 5 mm in diameter at anthesis, glabrous; style ca. 5 mm long (including stigmatic surfaces), straight; stigma yellow, bifid, the lobes 1.5–2 mm long. ***Fruit*** a berry, 20–25 mm diameter, globose; immature fruit green, fleshy; mature fruit light green, drying to yellow-orange or tan, becoming leathery-reticulate and bony hard and loosely retained and partly-enclosed in calyx (75% enclosed when developing; mature, hardened fruit less than 25% enclosed), apparently detaching from calyx once hard and dry. Fruiting calyx lobes 2.1–2.8 cm long, long acuminate, tapered to a long fine tip, accrescent, slightly sticky and adherent to fruit when immature, readily separating from fruit as the berry matures, hardens, and shrinks from drying, densely armed with sharp prickles ca. 6 mm long. ***Seeds*** up to 420–586 per fruit in cultivation (two wild-collected fruits were $N = 96$ and $N = 162$), 1.1–1.5 mm in diameter, reniform dark brown to black, conspicuously and minutely reticulate.

Distribution and ecology. *Solanum scalarium* is presently known from a single population (Fig. 3) of perhaps 50–100 individuals found within Judbarra/Gregory National Park. The species here occurs on skeletal pink soil, exposed sandstone pavement and dissected rock high above the Victoria River Valley (Fig. 4). The associated vegetation at this site is a low open woodland dominated by *Corymbia terminalis* (F.Muell.) K.D.Hill & L.A.S.Johnson (Myrtaceae) and *Eucalyptus miniata* (F.Muell.) A.Cunn. ex Schauer (Myrtaceae), with a sparse low mid story of *Owenia vernicosa* (F.Muell.) (Meliaceae), *Calytrix exstipulata* DC. (Myrtaceae), *Xanthostemon paradoxus* (F.Muell.) W.J.Hooker (Myrtaceae), *Hibbertia* spp. (Dilleniaceae), *Corchorus* spp. (Malvaceae), *Senna oligoclada* (F.Muell.) Randell (Fabaceae), *Acacia* sp. nov. (Fabaceae); the sparse ground layer is dominated by *Cyperus cunninghamii* (C.B.Clarke) C.A. Gardner

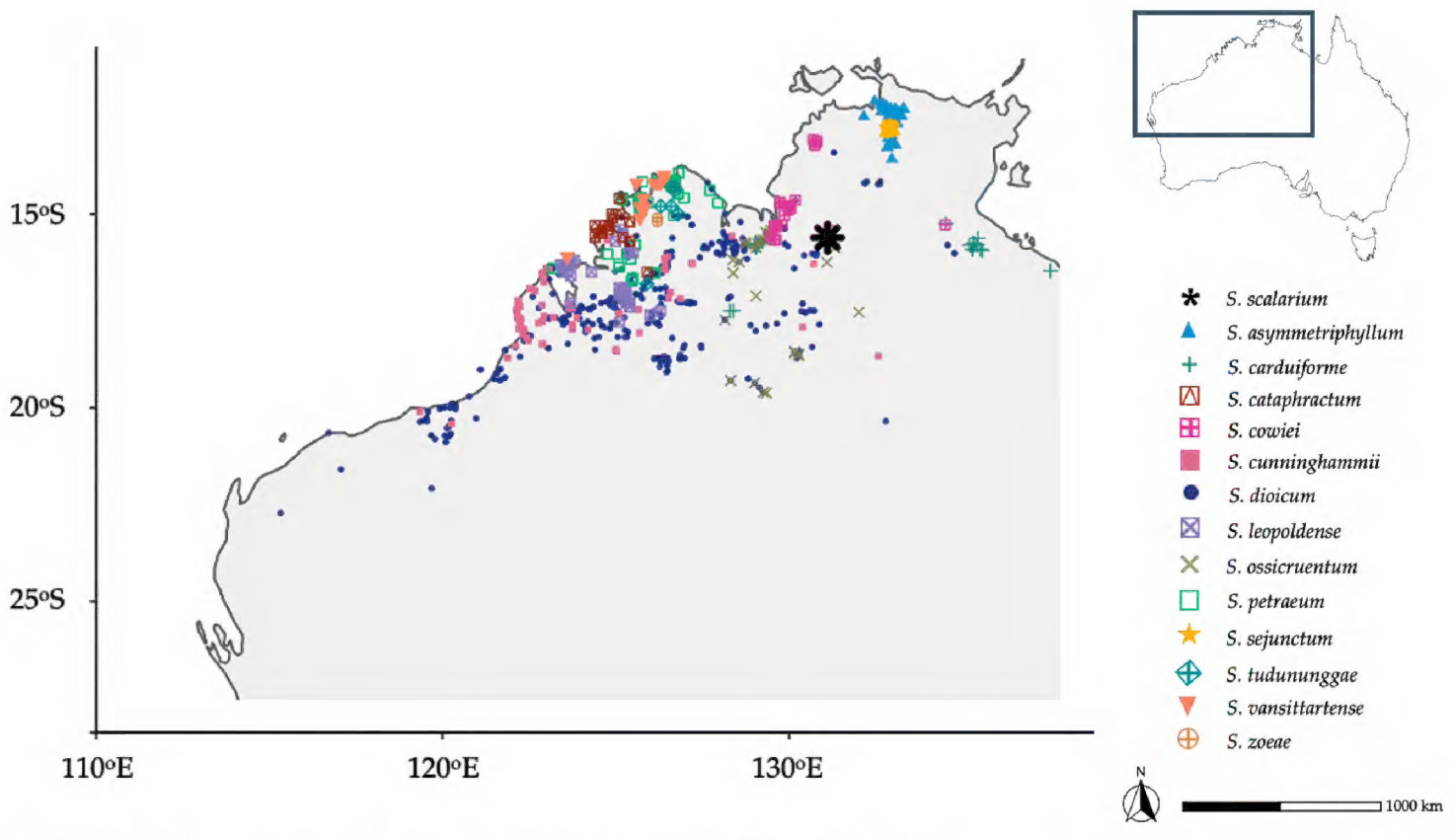

Figure 3. Geographic distribution of *Solanum scalarium* (black star) and other Australian dioecious *Solanum* species (source: The Australasian Virtual Herbarium).

Figure 4. *Solanum scalarium* in the field **A, C, F** type locality and habitat, Escarpment Walk, Judbarra National Park, Northern Territory **B–D** immature green fruits enclosed in prickly calyx and **E** prickly male rachis after male flowers have dropped off. (Photos by A.J. McDonnell.).

(Cyperaceae) and *Triodia pungens* R.Br. (Poaceae). Although *S. scalarium* was not conspicuous on a visit by PJ and JTC in 2017, it appeared in 2018 to have sprouted vigorously from above-ground stems after fire occurring at some point in the previous 2–3 years. At the time of the type collection, plants were robust and vigorous in areas that had been burned and only represented by a few weak ramets in unburned areas dominated by *Triodia pungens* tussocks.

Pollination biology of the species is unknown, but, like other Australian congeners, the flowers are likely buzz pollinated by bees in the genera *Xylocopa* and *Amegilla* (Apidae; see Anderson and Symon 1988; Switzer et al. 2016) and likely to present high levels of pollen nutritional reward – although with slightly differential rewards available to pollen foragers from male versus functionally female flowers (Ndem-Galbert et al. 2021). A small set ($N = 10$) of ex situ hand pollinations conducted for this study showed that inaperturate pollen produced by functionally female flowers does not lead to fruit set when used to pollinate other females. This suggests that reproduction in *S. scalarium* is dependent on intersexual male-to-female outcrossing via biotic pollination like in other dioecious *Solanum* species.

Seed dispersal mechanism for this species is also unknown, although young fleshy fruits are mostly enclosed in a spiny calyx that gradually reflexes to some degree as fruits become dry and bony (Fig. 6D, E), suggesting that endozoochory is less likely than

either ectozoochory (as a trample burr) or passive dispersal (see Symon 1979b; Martine et al. 2019). Peoples of the Walmajarri language area of the Kimberley region (west of this distribution) report that the fruits of *S. dioicum* (*kara*) are eaten by *Osphranter rufus* (Desmarest, 1822) (plains or red kangaroos; Doonday et al. 2013), and CTM has seen bustard birds (*Ardeotis australis* (Gray, 1829)) picking apart *S. dioicum* fruits near the northwest Kimberley coast (Martine et al. 2019). However, there is no published evidence that any extant animal acts as an effective seed dispersal agent of taxa within the "Kimberley dioecious clade" (see Martine et al. 2016b). Notably, seeds removed

Figure 5. Functionally male individuals of *Solanum scalarium* in cultivation: **A** leaf shape and **B, C** inflorescence axes of male individuals; note the distinctive spreading straight prickles that give the inflorescence axis a ladder-like appearance. (Photos by T.M. Williams.).

Figure 6. Functionally female individuals of *Solanum scalarium* in cultivation: **A** flower **B** reproductive branch **C** leaf shape **D, E** reflexing of calyx around brown, bony fruits and **F** overall habit. (Photos by T.M. Williams.).

Figure 7. A Holotype of *Solanum scalarium* (C.T. Martine 4748; female fruiting specimen) **B** paratype of *S. scalarium* (C.T. Martine 4796B; male specimen). (Photos by M. Sain.).

from green fruits (enclosed in calyces) of the type collection as well as seeds removed from older brown fruits (calyces reflexed) in cultivation were both germinable, suggesting that effective seed dispersal might happen at either stage.

Phenology. Plants encountered on 2 June 2018 were largely sterile, with several withered flowers and two mature fruits. The low fruit set in the population at the time of collection suggests that *S. scalarium* typically flowers earlier in the calendar year.

Etymology. Latin *scalare* from *scala*, ladder or stair, and suffix *aris*, pertaining to; the epithet *scalarium* is the genitive plural of *scalare*, indicating ladder-like appearance of staminate inflorescence rachises, which are conspicuously and unusually armed with relatively stout, spreading, straight prickles resembling ladder steps. It is also a nod to the type locality at the Escarpment Walk, Judbarra/Gregory National Park, where stone stairs lead from the car park up to the habitat of this species. By choosing this name we acknowledge the access these steps provide to the newly-described species as well as the importance of providing broad access to nature, outdoor recreation, and scientific discovery. We suggest the use of Garrarnawun Bush Tomato for the English-language common name of the species in recognition of the Garrarnawun Lookout near where the type collection was made, a traditional meeting place of the Wardaman and Nungali-Ngaliwurru peoples whose lands overlap in this area (Parks and Wildlife Commission of the Northern Territory 2021).

Preliminary conservation status. While we expect that more localities for *S. scalarium* are likely to be found given the prevalence of similar (and less accessible) outcrops in the immediate region of the type collection, at present it is known from one protected (though frequently-visited) collection site in Judbarra/Gregory National Park (Fig. 4). Based on IUCN Red List Categories (IUCN 2012), *S. scalarium* should be considered Data Deficient (DD).

Specimens examined. United States. Pennsylvania: Cultivated in Bucknell University: (Lewisburg) Burpee Research Greenhouse (staminate flowers/inflorescences, functionally female flowers, and fruits), 9 Oct 2020*CT Martine & TM Williams 4796.* (To be distributed to AD, BM, BUPL [Fig. 7b], DNA, NY, PERTH, US).

Diagnostic couplets. A comprehensive "Kimberley dioecious clade" key, including newly-recognized species, is forthcoming (Barrett and Barrett in prep). The most complete key to date can be found in Barrett (2013), which lumps the numerous variations of *S. dioicum* sensu lato as a single taxon. The following couplets may be inserted where *S. dioicum* occurs at couplet 60 in the key in Barrett (2013) and supplants the single replacement couplet 60a [previously published in Martine et al. (2016c)].

[Barrett 2013; couplet 60]

60a Plants less than 1 m tall, many-branched; stems moderately to densely prickly; leaf indumentum silvery/rusty/yellow, overall aspect silvery-green, yellow-green, or reddish-green; stigma deeply bifid, the lobes 2–5 mm long; calyx not fully enclosing mature fruit.....**60b**

60a Plants more than 1 m tall, few-branched and conspicuously "Y"-shaped in form; stems very prickly; leaf indumentum silvery, overall aspect silvery-blue; stigma shallowly bifid, the lobes 0.5–1 mm long; calyx fully enclosing the mature fruit ..... ***Solanum ossicruentum*** **Martine & J.Cantley**

60b Plants many-branched; stems moderately prickly; leaf indumentum silvery or rusty, overall aspect silvery-green, yellowish green, or reddish green; stigma lobes 2–5 mm long; mature fruits green and fleshy; male floral rachis typically unarmed ..... ***Solanum dioicum*** **W.Fitzg.**

60b Plants many-branched and spreading decumbent in form; stem densely prickly; leaf indumentum yellow, overall aspect yellow-green; stigma lobes 1.5–2 mm; mature fruits light green to yellow-orange and fleshy, becoming tan and bony hard; male floral rachis armed.....
.....***Solanum scalarium*** **Martine & T.M.Williams**

Discussion

Solanum scalarium is the latest in a series of newly-described functionally dioecious species from the "Kimberley dioecious clade" (see Martine et al. 2011, 2013, 2016c; Barrett 2013) a group that is still rife with undescribed species lumped under the umbrella of *S. dioicum* (Barrett 2013). Although some of the variation within the clade

is subtle and/or continuous, *S. scalarium* can be distinguished from all known members by the combination of spreading decumbent habit and male inflorescence rachis armed with relatively stout, spreading, straight prickles. Complex habitat and environmental characteristics, coupled with climate fluctuations over the last two million years, have been drivers of the high species diversity and speciation events throughout Australia (Bowman et al. 2010; Edwards et al. 2017; Edwards et al. 2018). There are particularly high levels of plant diversity and newly described species within the AMT (Bowman et al. 2010; Barrett 2013; Edwards et al. 2017; Edwards et al. 2018; Martine et al. 2019).

Forthcoming phylogenomic work (e.g., McDonnell and Martine in prep) should aid in resolving what has been a decades-long effort to gradually assign species names to recognizable local forms in this complex group. In the meantime, the best course of action continues to be collecting all forms of "*Solanum dioicum*" when they are encountered such that the variation within the group continues to be captured in herbarium collections (see Heberling et al. 2019; Thiers 2020).

The scientific name and English-language common name proposed here acknowledge the critical importance of maintaining equitable and safe access to outdoor spaces, the Garrarnawun Lookout being a poignant example of shared use of special places.

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